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# STUDIES OF LOCALIZED STAGES IN SOME PLANTS OF THE BOTANIC GARDENS OF HARVARD UNIVERSITY.

JOSEPH A. CUSHMAN.

In animals and plants interesting stages occur at certain parts throughout the life of the individual. These are expressed in Jackson's law, "Throughout the life of the individual, stages may be found in localized parts, which are similar to stages found in the young, and the equivalents of which are to be sought in the adults of ancestral groups." In a preceding paper the author has described such localized stages in some New England plants. In the present paper the same line of investigation has been extended to certain exotic plants which have been recently studied. Jackson showed that such localized stages occur in organisms at very definite areas and under definite conditions of growth. This view is corroborated by the present study.

My thanks are due to Prof. G. L. Goodale and Dr. E. W. Olive for supervising my work, to Mr. Cameron for opportunities to study a great number of seedlings in the greenhouses and for the care of those under observation, and to Dr. Jackson for reading this paper and for many helpful suggestions.

The following examples show the various ideas here intended to be brought out in the line of localized stages in development.

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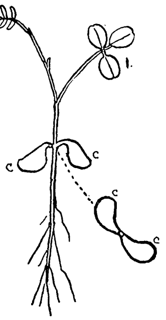
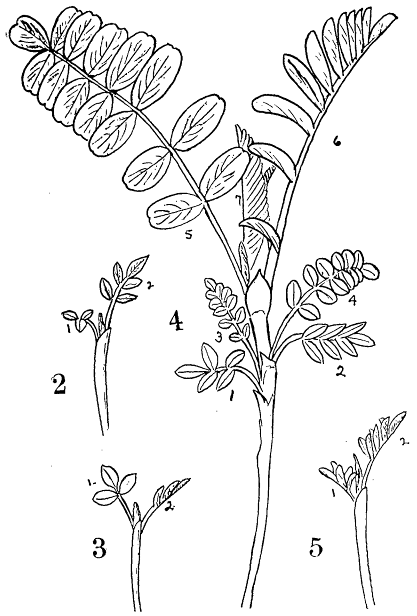


FIG. 1. Seedling of *Astragalus adsurgens*, showing cotyledons *c*, *c*, and first and second nepionic leaves, the first with 3, the second with 5 leaflets.

## **Astragalus adsurgens** Pall. Figs. 1–5.

This herbaceous plant, a native of Siberia, shows in its early spring growth localized stages in development. The leaves are compound and so the differential characters are more easily and definitely seen than in many plants. Seedlings (Fig. 1) were obtained beneath the adult plants which were at that time — April — just appearing. The cotyledons are comparatively large, green and fleshy, with a peculiar one-sided appearance. The leaves are alternate, the first nepionic leaf having three leaflets, the second five. In some cases the third leaf had five leaflets like the second leaf and in other cases seven, the greater number having five. This shows as noted in the previous paper (Studies of Localized Stages of Growth in some Common New England Plants," *Amer. Nat.*, Vol. 36, No. 431.) a difference in acceleration of development in individual seedlings. An interesting feature of the leaves is the fact, as was mentioned in the preceding paper, that the tip of the later leaves repeats the form of the tip of the first leaf. In looking over the figures of this plant it will be noticed that the tips of all the leaves do not correspond as shown especially in Fig. 4. This seems at first sight an exception to the principle of localized repetition, but on careful study was seen to be due to the following growth. The first few leaves seem to have a further development after unfolding. At first the tip is as given in Figs. 2, 3, and 5. Then later the tip broadens and becomes distally notched. This is seen also in the seedling, when the leaf unfolds the tips being pointed but afterward becoming reëntrant as noted in Fig. 4. The first leaves of seedling and spring growth then are retarded even in taking on such a character as the shape of the tip.



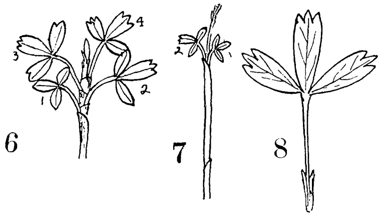
FIGS. 2–5. Spring growths of *Astragalus adsurgens*, figs. 2, 3, 5 weak growths, fig. 4 stouter more vigorous growth.

In early spring growth the first leaves of weaker shoots are trifoliolate as in Figs. 2 and 3. Where this is the case the second leaf is usually of five leaflets. These two leaves then correspond exactly with the characters seen in the seedling. In stronger growths, however, the first leaves have five leaflets or even more. The second in such cases usually have seven.

Fig. 4 shows exceptionally well a series of stages in early spring growth. The first leaf has five leaflets, the second seven. The third leaf which is in the axil of number 1 has eleven leaflets; the fourth, in the axil of number 2 has thirteen. Number 5 farther up the stem has fifteen, number 6 twenty-one. Number 7 which is not wholly unfolded shows that it will have many more than the leaf preceding it. The specimen represented by Fig. 4 was taken from one of the strongest growths found and does not revert to the very first condition of the leaflets found in seedlings or feeble growths, as that in Figs. 1, 2, and 3. In Fig. 4 there would naturally be a stage between leaves 2 and 3 with nine leaflets. In the strong growths these intermediate steps are very apt to be skipped by acceleration of development. Such a stage however is found in specimens such as represented by Figs. 2, 3 and 5. The similarity of the early spring growths representing localized stages to the seedling representing direct development is strikingly shown in such plants as this where the number of leaflets may be actually counted.

### **Potentilla tridentata** Ait. Figs. 6–9.

Seedlings of this plant were found in the spring about the adult plant and were alike in having the first nepionic leaf trifoliolate, but differed in the characters of the tip of succeeding leaves. The first nepionic leaf has no distal notches and is almost exactly like the first leaf of Figs. 6 and 7. The second leaf is very variable, it may repeat the characters of the first leaf exactly or the tip may be tridentate on all three leaflets or on the terminal one only. When the terminal leaflet is tridentate the lateral leaflets may be simple like leaf 2 of Figs. 6 and 7, or may have a single



FIGS. 6–8. *Potentilla tridentata.* Figs. 6 and 7 early spring growth. Fig. 8 typical species leaf.

notch as in leaf 3 of Fig. 6. The typical leaf of the adult plant has all three lobes tridentate at the tip — Fig. 8.

This species in its direct development is more accelerated than others in the genus. Turning to Lubbock's "Seedlings" '92, there are figured *Potentilla fulgens* Wall, Vol. 1, p. 488, Fig. 315 and *P. repetens* L., p. 487, Fig. 314, in which the first two nepionic leaves are simple, the third trifoliolate. In *P. anserina* L. and *P. bifurca* L. the first leaf only is simple, the second trifoliolate. Here then is a distinct difference in the rate of acceleration, our species noted here having the first leaf trifoliolate.

A large majority of the first leaves in spring growth show excellent localized stages. Usually the first leaf is trifoliolate with simple tips on all the lobes as in Figs. 6 and 7. This is exactly like the first nepionic leaf of the seedling. The most common condition for the second leaf of spring growth, on weak shoots especially, is a tridentate tip on the terminal lobe and a simple one for the lateral lobes. The third leaf may take on the full specific characters or may have the lateral lobes with a single notch as in leaf number 3 of Fig. 6. We have then in Fig. 6 a shoot which repeats all the stages seen in the various seedlings mentioned. It is a sort of ideal condition, repeating all the stages of the seedling of the same plant, in the proper sequence without repetition.

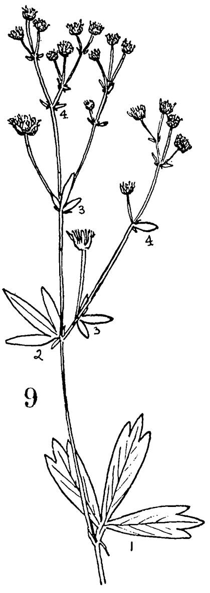


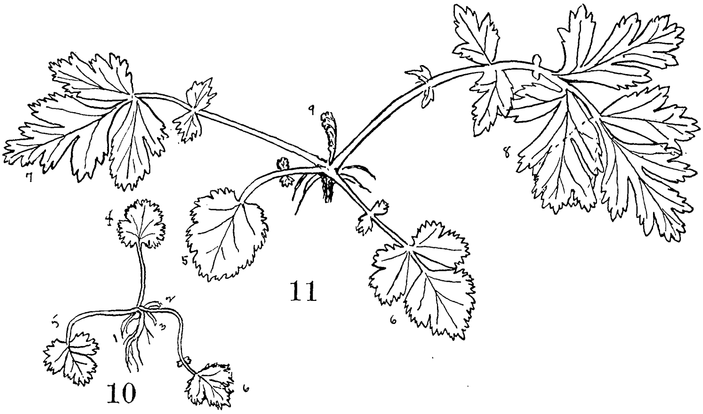
FIG. 9. Fruiting stalk of *Potentilla tridentata* showing localized senescence due to loss of strength in flowering and fruiting.

The stages beneath the flower or as shown here beneath the fruit, Fig. 9, repeat in the reverse order the stages noted in the straight development of the seedling and in the localized development of the early spring growth. Above the highest typical leaf is one which is like the first leaf of the seedling and first leaf of spring growth, being a trifoliolate leaf with tips which are simple. After one or two leaves of this type the leaf drops the lateral lobes and becomes a simple unifoliolate leaf to the base of the highest flower cluster. This last condition is a simpler and therefore more reversionary character than any found either in the seedling or the early spring growth. This may be compared to what is seen in simpler species as figured by Lubbock, *P. repetans* L. and others as mentioned above in which the first nepionic leaf is simple although dentate in outline. *Potentilla tridentata* may therefore be considered accelerated in development in that it has skipped the simple leaf stage in early development. It is an important fact that in the ontogeny of the individual the simplest stage found occurs not in the young but as a definite feature of localized senescence.

### **Geum virginianum** L. Figs. 10, 11.

Of this species seedlings were not obtained, but the early leaves in other species as figured by Lubbock (*Geum freemontii* Hort. and *G. coccineum* Sibth. and Sin. Vol. 1, p. 486, fig. 313) are orbicular with varied dentations, more or less deeply cut.

In early spring growth of adults the first leaves are of this same character. In the specimen, Fig. 10, the first three leaves



FIGS. 10–11. *Geum virginianum*, spring growths from the ground.

had dropped off before it was drawn. The fourth leaf has the orbicular form like the seedlings as noted but begins to show a three-lobed character by the deeper notches on the sides. The fifth is deeply cut and the trilobate character much stronger. The next leaf number 6 is not only trilobate but has begun to develop the next pair of leaflets proximally. Fig. 11 shows a stronger growth with the same main features. Leaf number 5 although it has begun to develop the second pair of leaflets still holds to the rounded form in the terminal leaflet. The next leaf, number 6, however has become more split up and successive developments of this character are shown in numbers 7 and 8. The proximal part of the leaf here shows a failure to develop full characters as seen in the more simple leaflets toward this part.

Beneath the flower there is a gradual reduction of these characters and a return to leaves much like those of earlier growth as shown both in the seedling and in the early spring growth, the stages being in the reverse order of sequence.

### **Lamium sp?** (Dead Nettle). Figs. 12–18.

In the seedlings raised, Fig. 12, the cotyledons were foliaceous, glabrous, petiolate; lamina oblong-reniform, deeply cordate at the base with a slight distal median notch; petiole nearly terete, slightly flattened above. The petioles become much elongated and grow upward for some time with their bases nearly touching, petioles in specimens raised were an inch long two weeks after germination. The first nepionic leaves are opposite and at this time seem apparently sessile as the strength seems to be used in the lengthening of the first intermode; later they become petiolate. This is a progressive development of the proximal portion during growth. These first leaves have an orbicular form, crenate at the margin, a terminal rounded tooth and from two to four lateral teeth on a side. Following leaves increase the number of the lateral teeth and the broadest part of the leaf moves toward the base.

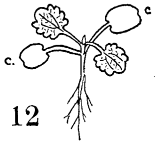


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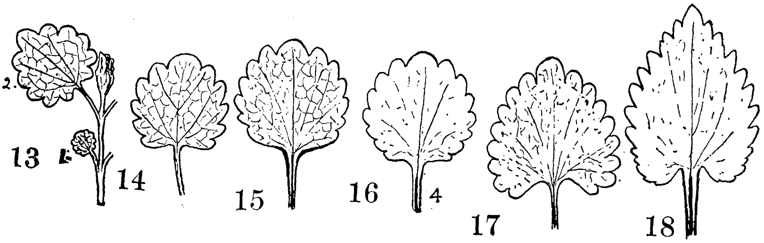
Fig. 12. Seedling of *Lamium* c. c. cotyledons, first two nepionic leaves.

In spring growth, Fig. 13, the first leaf was very similar to the first nepionic leaf figured, Fig. 12. The number of teeth was the same and the general orbicular form of the leaf. The second leaf, Fig. 14, has another tooth added and the broadest part of the leaf is nearer the base than in the first leaf. The remaining leaves, Fig. 15–18, show the increase in the number of the teeth, the migration of the greatest breadth to near the base of the leaf, the cordate form of the base and the change in the tip as well as of the whole leaf in becoming more pointed.



Figs. 13–18. Progressive stages in spring growth of *Lamium* showing increase in number of notches and gradual auricled form of the base with a pointed form of the whole. Compare with leaf 1 of fig. 13, the nepionic leaves of fig. 12.

At the upper part of the flowering stalk the leaves decrease in the number of teeth until the highest leaves are simple and lanceolate, usually with a clasping base repeating in reverse order of sequence stages seen in the seedling and young growth of early spring, becoming even more simple.

### **Artemisia stelleriana** Bess. Fig. 19.

Although the seedling of this species was not obtained, other species which have few-lobed leaves as figured by Lubbock (Vol. II, p. 135.) *Artemisia annua* L. and *A. mutellina* Vill. have a development much like what is represented in Fig. 19. In the early spring growth which is figured, the first four leaves are simple becoming progressively spathulate in succeeding leaves. The next four are three-lobed and after that the five-lobed character appears, representing the greatest complexity reached in the species. The lobes in later leaves are much separated but do not increase in number.

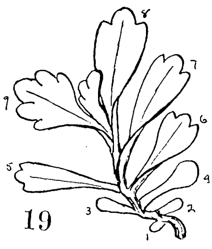


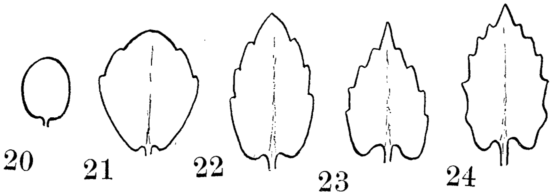
Fig. 19. Spring growth of *Artemisia stelleriana* showing progressive stages in reaching the typical five-lobed leaf.

In weak and late growths there is a return to earlier conditions, it being true localized senescence, appearing late in the season at the end of the season's growth.

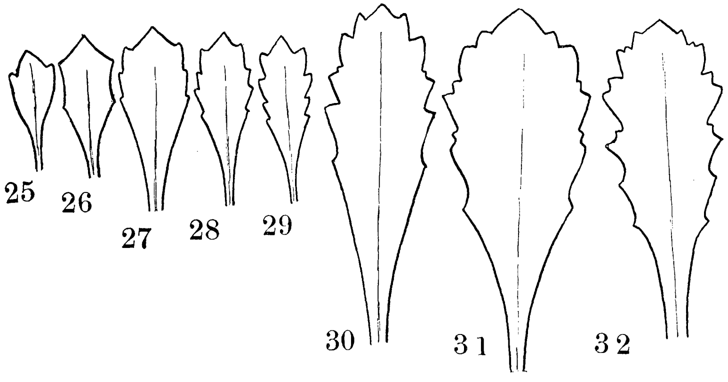
The lobes are frequently progressively reduced to three and in rarer instances to the simple form shown at the base of spring growth. Here then where there is no flower to take the strength of the plant from the leaves, the diminutions of growing strength near the end of the season is sufficient to bring out regressive characters.

### **Arabis albida.** Figs 20–37.

The seedlings of this plant have after the cotyledons a simple rounded-oval leaf rounded at the base, Fig. 20. The second leaf is broadly ovate with the widest part at about the middle, four slight notches making two teeth on each side, very slightly raised from the general outline and an auricled base, Fig. 21.



Figs. 20–24. Stages in seedling of *Arabis albida* and may represent also the stages seen in shoots from the ground in spring growth as the two are so nearly identical.

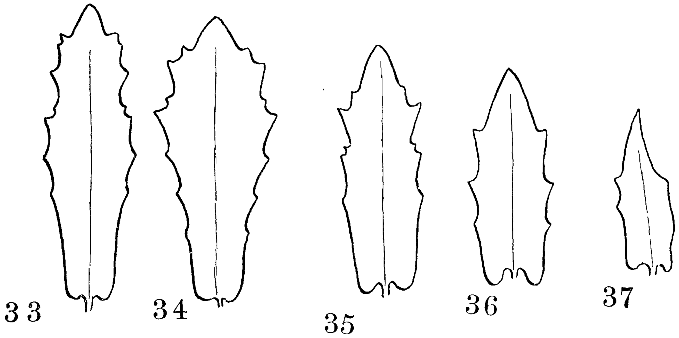


Figs. 25–32. Stages in spring growth of *Arabis albida* from stems of preceding years growth. These early leaves do not have the auricled base of the early growth from underground.

The third leaf is broadest nearer the base, more pointed and with three teeth on each side, the base auricled, Fig. 22. The fourth leaf has a still more pointed form, the widest portion still nearer the base which is now deeply auricled, Fig. 23. The fifth leaf has still more lateral teeth, Fig. 24, and so on.

The spring growth of this plant is of two distinct kinds. In one the shoots come from underground and are succulent, growing rapidly with long internodes, in the other the growths come from the part of the plant above ground which survived from the previous year. This growth is not so rank and the internodes are much shorter; a decided difference in the leaves of the two forms is noted.

In the growth from underground the stages passed through may be represented by the figures of leaves of seedlings, Figs. 20–24, the stages being exactly comparable to those of the seedling. In the growth from above ground, however, there is a decided deviation from this form. The earliest leaves are tapering to the petiole and with but one tooth on a side, Fig. 25. The second leaf has two teeth on a side but decidedly different from those of leaves from underground shoots. In both however the widest portion is near the distal end. The growth continues, Figs. 26–29, with the number of teeth increasing and becoming doubly serrate, Figs. 30–32. The greatest width continues to be at the top.



FIGS. 33–37. Continuation of stages on same stalk as preceding series but nearing the flower, fig. 37 being the last leaf before reaching the flower. These all revert to the auricled base of the seedling.

Beneath the flower however the leaf changes in its characters. The base becomes auricled, Fig. 33, like the leaves in the seedling and in the growth from the ground. Also the greatest width moves toward the proximal end, the number of dentations decreases until in Fig. 36 there are but three on each side and in Fig. 37 there are but two, in form very much like Fig. 21, the second leaf of early growth from the ground. Its base is auricled like the seedling and early growth from the ground and the upper part is like the growth from old shoots.

### **Poterium canadensis** A. Gray. Figs. 38–41.

Early in the spring seedlings of this plant were obtained about the adult. They were taken up and grown in pots in order to study variation in the first leaves. The seedling, Fig. 38, develops as follows: the cotyledons are broadly oval, nearly orbicular, obtuse, deeply cordate at the base, glabrous, subfleshy, deep green with petiole subterete, slightly channeled above. The first nepionic leaf is pinnately trifoliolate, leaflets petiolate, rotund, incise-serrate, lateral ones sub-cordate at base, tip with smaller and

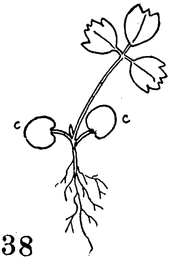


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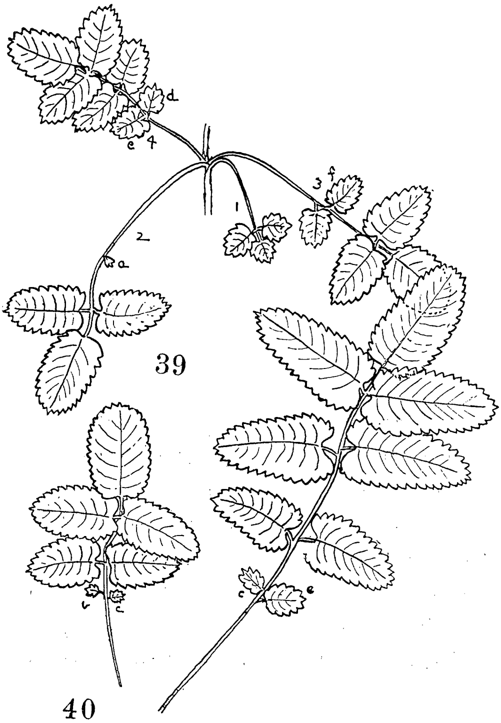
FIG. 38. Seedling of *Poterium canadense* showing cotyledons c. c. and first nepionic leaf.



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FIGS. 39, 40. Early leaves of *Poterium canadense.* The leaflets lettered from *a* to *f* show localized stages in separate leaflets and the senescent character of the proximal portion of the leaves.

shorter serrature than the others. Usually the lateral leaflets were like the terminal but in some cases were more complicated, Fig. 38, having five teeth in the lateral and three in the terminal leaflets.

In early spring growth from mature plants, localized stages are seen especially well-marked in weaker lateral shoots from the side of the clump. One such is figured, Fig. 39. The first leaf was like the first leaf of the seedling except that it had a greater number of teeth on each of the leaflets. The second leaf was mainly trifoliolate with a trace of the second pair of leaflets at *a*, which is noteworthy as it is like the leaflet of the seedling in having three teeth. The third leaf has five leaflets and the fourth seven. The later leaves increase the number of leaflets until there are as many as twenty three or even more in a single leaf. In the developing leaf the proximal part is the last formed and oftener shows characters which, being a failure to develop the full characters, may be compared to the young and considered as localized senescence, in that individual leaf. Similar localized reversion of the proximal part of leaves were shown in the previous paper mentioned (*Amer. Nat.*, Vol. 36, No. 361) in Tansy and here also in Geum. They are shown in *Gymnocladus disicus* by Dr. Jackson (*Mem. Bost. Soc. Nat. Hist.*, Vol. 5, No. 4. "Localized Stages in Development in Plants and Animals"). These proximal reversionary leaflets repeat various stages in the development of the typical leaflet of the plant as shown in leaves lettered *a* to *f* in Figs. 39 and 40. Leaflets in this part of the leaf may be found representing various steps from the tridentate character at *a* which is typical of the first nepionic leaf to one of thirteen teeth at *f* comparable to a much later stage in seedling growth. These leaves also approach nearer to the earlier leaflets in having less auricled bases, a character which is especially noted in the seedling. The leaflets in the adult show an overlapping in the distal portion and distinct separation in the proximal.

The stages beneath the flower are definite and easily made out. From a typical leaf having a great number of leaflets, in succeeding leaves the number becomes gradually reduced until at some distance below the flower leaves are found having nine leaflets or fewer. In the specimen figured the reduction has produced at the base a leaf of seven leaflets. From this stage the reductions following the figure, are as follows, Fig. 41. At the base no. 1 is a leaf of seven leaflets. The lower pair of leaflets in this leaf is somewhat changed so that they have almost the character of stipules. This shows that the reduction should be thought of as a failure to develop characters, even the distal half of these two leaflets being much nearer the usual form than the proximal half. The teeth on the distal side are well developed and the lateral secondary veins show well, while on the proximal side the teeth are few and poorly developed and the veins are not distinguishable. By the shortening of the proximal side by its weaker development, the whole shape of the leaflet is changed and greatly aborted from its usual form. The same modification of proximal leaflets is characteristic of leaves below the flower in other plants. To continue with the development toward the flower, number 2 will be seen to have lost this third pair and the second pair has assumed a like abortive character. Here the whole proximal half is without teeth. This simple part of the lowest pair of proximal leaflets has varying degrees of reduction in different cases. The leaf number 3 has been reduced to three

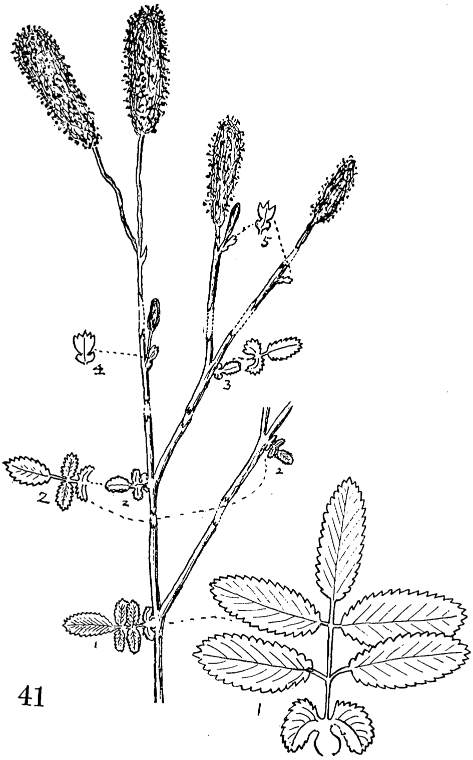

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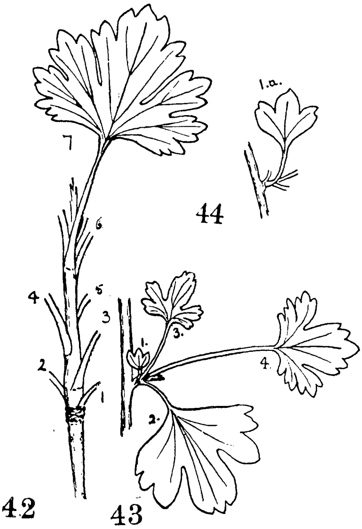
FIG. 41. Flowering stalk of *Poterium canadense* showing localized senescence below the flower. Breaks in the stem are simply to allow its being put into smaller space. Leaves 1–5 enlarged to nat. size.

leaflets, the lower two of which have assumed the same abortive form as described. Leaf number 4 has simply the terminal leaflet and that greatly reduced in number of dentations. Number 5 has but three dentations characteristic of the terminal leaflet of the first nepionic leaf but the lateral proximal border expanded in a manner suggestive of the proximal modification of preceding leaves.

These stages are exactly comparable to the stages of the seedling and early spring growth in number of leaflets. In this reduction as noted before in other plants, stages are developed as in numbers 4 and 5 which are simpler than any shown in the direct development of the seedling or in the localized development shown in early spring growth. This is again a case of repeating stages in the reverse order from that of the seedling and early spring growth.

### **Ribes aureum** Pursh. Figs. 42–45.

This plant which is grown quite extensively as a garden shrub shows excellent localized stages in its spring growth on all parts of the plant as well as below the flower. The flowering season is early and the very earliest leaves are persistent enough so that they are still on the plant and can be compared with stages beneath the flower. In some cases among the lowest shoots which bear flowers the series can be traced entire in the growth from one bud, from the simplest early leaf to the complex and back through the simple again to the flower.



Figs. 42–44. Spring growth of *Ribes aureum*. Fig. 42 most complicated leaf attained by the species.

In early spring growth the simplest leaf usually found is like leaf 1 of Fig. 43, a leaf with three lobes and tri-nerved. The next leaf is more decidedly trilobed but with a division into teeth. The next leaf has the lower lobes divided and this division becomes somewhat more marked in later leaves until the most complicated leaf is developed as in leaf 7, Fig. 42. In Fig. 44 is shown a leaf intermediate between leaves 1 and 2 of Fig. 43. By obtaining more specimens a more complete series may be secured between many of the stages. In Fig. 43 a significant thing is shown in the size of leaf 2. The first leaf grew under unfavorable conditions and its development in size went but a little way. The weather changed however and became warmer while leaf 2 was developing and its unusual size is the result. Next it was colder and leaves 3 and 4 felt the effect. This was noticeable in many cases at this particular time.

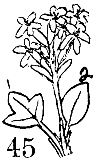


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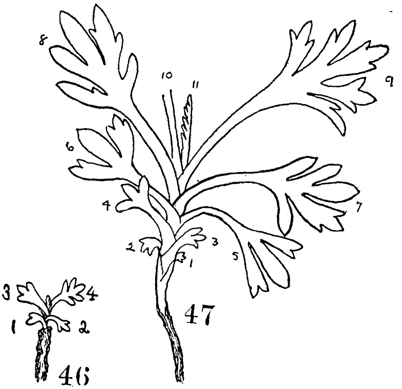
FIG 45. Leaves of *Ribes aureum* below the flower.

Turning to the flower Fig. 45, the leaves are reduced as shown in the lowest leaf figured to leaves corresponding to Fig. 43, leaf 1. But as in the cases mentioned before, the reduction is carried still farther as leaf 2 is simple in outline with no traces of the teeth or lobes of the simplest leaf of spring growth. This simpler form is found in a great number of cases in the last leaf below the flower. As in cases previously mentioned this stage is simpler than in its own young.

### **Chrysanthemum speciosum.** Figs. 46, 47.

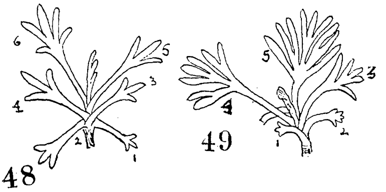
The seedling of this species repeats the essential steps shown in Fig. 47 of the spring growth, but less completely. In the early spring growth more stages are represented. A very weak growth is shown in Fig. 46. In this the first leaf was nearly simple having a lobe on one side only. The next leaf was three-lobed and the following also. The fourth was five-lobed. In a stronger growth, Fig. 47, the first leaf was three-toothed, the lobes being simply teeth and nothing more. The next three were simply three-lobed and the fifth and sixth instead of having five lobes produced a complication of the lower pair of lobes. These have two teeth in leaf five and in leaf six one has the characteristic three-toothed form. In the remaining leaves the five-lobed character is shown and the lobes usually each assume a three-lobed character in which each lobe is comparable to the first leaves of Fig. 46.



FIGS. 46, 47. Early spring growths of *Chrysanthemum speciosum.*

Beneath the flower the plant repeats, in the reverse order, these stages with great definiteness. Beginning with the typical complicated leaf at the base of the flowering branch, stages are represented gradually losing their characters in the reverse order to the development figured, until simple five-lobed leaves are reached, then three-lobed ones and finally beneath the flower are simple leaves which are even simpler than the first leaves of the seedling. The reduction is complete and exactly retraces the stages of the seedling and early spring growth as localized senescence.

## **Artemisia abrotamum** (Tourn.) Neck. Figs. 48, 49.

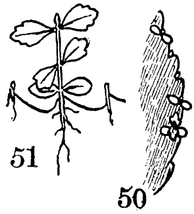


FIGS. 48, 49. Two examples of early spring growth in *Artemisia abrotamum* showing different degrees of acceleration.

In this species of the genus before given, Fig. 19, the leaves become much more complex in their lobing and the plant frequently blossoms. Seedlings were raised, the first nepionic leaves being three-lobed, the next five-lobed and so on. In the spring growth figured, Figs. 48, 49, the first leaves are three-lobed, Fig. 48, leaves 1–5, Fig. 49, leaf 1. The next leaves are five-lobed, Fig. 48, leaf 6, Fig. 49, leaves 2, 3. Then comes a splitting up and complication of lobes until the adult leaf is much dissected. Below the flower the return in the reverse order to simple condition is perhaps as well marked as in any case yet given. The return to a five-lobed leaf, then a three-lobed leaf, and finally to a simple leaf beneath the flower, a condition simpler than any seen in the seedling or spring growth as in so many other cases. This species is a good one for studying localized stages as the leaves are much cut up and pass through many, but nevertheless definite, stages.

### **Bryophyllum tubiflorum** Harv. Figs. 50, 51.

This plant is known to many by its power of reproducing by buds from the notches of the sides of the leaf. When a leaf is placed on damp sand or earth a bud soon starts out from each of these lateral notches, and young plants result, some showing greater strength than others. The leaf shrivels and finally dries up leaving a ring of new plants. These young plants show localized stages comparable to the seedling. One of the growths from such a leaf bud is shown in Fig. 51. The first pair of leaves are entire, the second have a single notch on each side, the third two on a side and so on. This repetition of characters is as strong as any seen in early spring growth.



FIGS. 50–51. Growths from leaf in *Bryophyllum tubiflorum*.

In the study of localized stages in development, as also noted in the preceding paper, in the study of spring growth the leaves of weaker shoots seem to be better than more vigorous ones for study as they repeat the greatest number of stages and revert to more primitive characters. Not only is this tendency to a repetition of characters found in spring growth from the ground, but also from the stems of the preceding year's growth and even as in the last case noted in growths from the leaves themselves.

In the leaves of flowering shoots or weak terminal growths at the end of the season the same stages are passed through as in the seedling or spring growth but always in the reverse order of sequence. This which is considered localized senescence is directly comparable to senescence of the whole individual as shown by Prof. Hyatt in his studies of cephalopods. In several cases described it is shown that beneath the flower the leaves are much simpler than in the seedling as shown in *Potentilla tridentata*, *Ribes aureum Poterium canadensis* and others. Such extreme reversion may be compared to the young of other species in the genus in which the first leaves do have more primitive simplicity.

This life history of a plant marked by stages in the leaves can be made out in many, perhaps all plants where the leaves are compound, notched or lobed and even sometimes where the leaves are entire, by changes in venation and outline.

CAMBRIDGE, MASS.
January.